MOULTS OF *DAKOTICANCER OVERANUS*, AN UPPER CRETACEOUS CRAB FROM THE PIERRE SHALE OF SOUTH DAKOTA

by GALE A. BISHOP

ABSTRACT. Of 4,000 specimens of fossil decapods collected from three stratigraphically different localities in the Pierre Shale (Upper Cretaceous, Maestrichtian) of South Dakota, twenty specimens of the brachyuran *Dakoticancer overanus* Rathbun were found preserved in Salter's position. Several of these specimens have the portion of the carapace which lies outside pleural sutures still attached to the sternal plastron, proof that they are exuviae. The part of the carapace between the pleural sutures is completely overturned on each specimen and rotated on most specimens. The escaping movements of the moulting crab probably caused water currents which in turn caused the central part of the carapace to slip backward over the moulting foundation resulting in the new type of Salter's position.

DECAPOD crustaceans, encased in non-growing exoskeletons, must moult or periodically shed their exoskeleton in order to grow. Moulting is a continuous process in the life of decapods. Drach (1939) has defined several stages in this process (Table 1).

TABLE 1. Brachyuran moulting Cycle, summarized from Passano 1960 (after Drach).

Stage	*Name*	*Characteristics*	*Activity level*	*Feeding*	*Water %*	*Duration %*
A	Newly Moulted	Water absorption, mineralization	slight	none	86	2·0
B	Paper Shell	Endocuticle formation, chelae hard, tissue growth begins	full	starts	85	8·0
C	Hard	Main tissue growth, accumulation of organic reserves	full	yes	60	66+
D	Peeler	Epicuticle formed, Exocuticle secretion, skeletal resorption pleural sutures open	full to reduced	some to none	60 to rise	24
E	Moult	Rapid water uptake and exuviation	none	none	rapid rise	0·5

The shedding of the exoskeleton (Stage 'E') takes only a short time. The animal stands in its normal position. The carapace splits along lines of weakness called the pleural sutures (text-fig. 1 *a*, *b*). The part of the carapace between the pleural sutures remains hinged to the internal skeleton and flips upward and forward (into Salter's position) as the animal escapes from the old exoskeleton. The escape is made possible by a drastic water loss in soft tissues and throbbing muscular contractions. After moulting there is a rapid uptake of water in the soft tissues which causes the increase in size of the animal.

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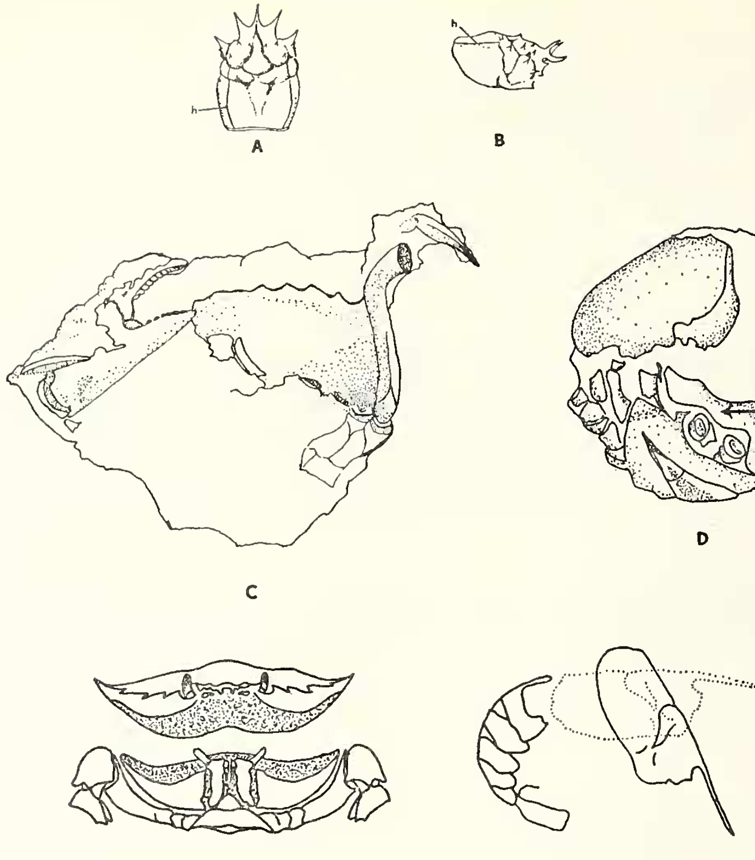
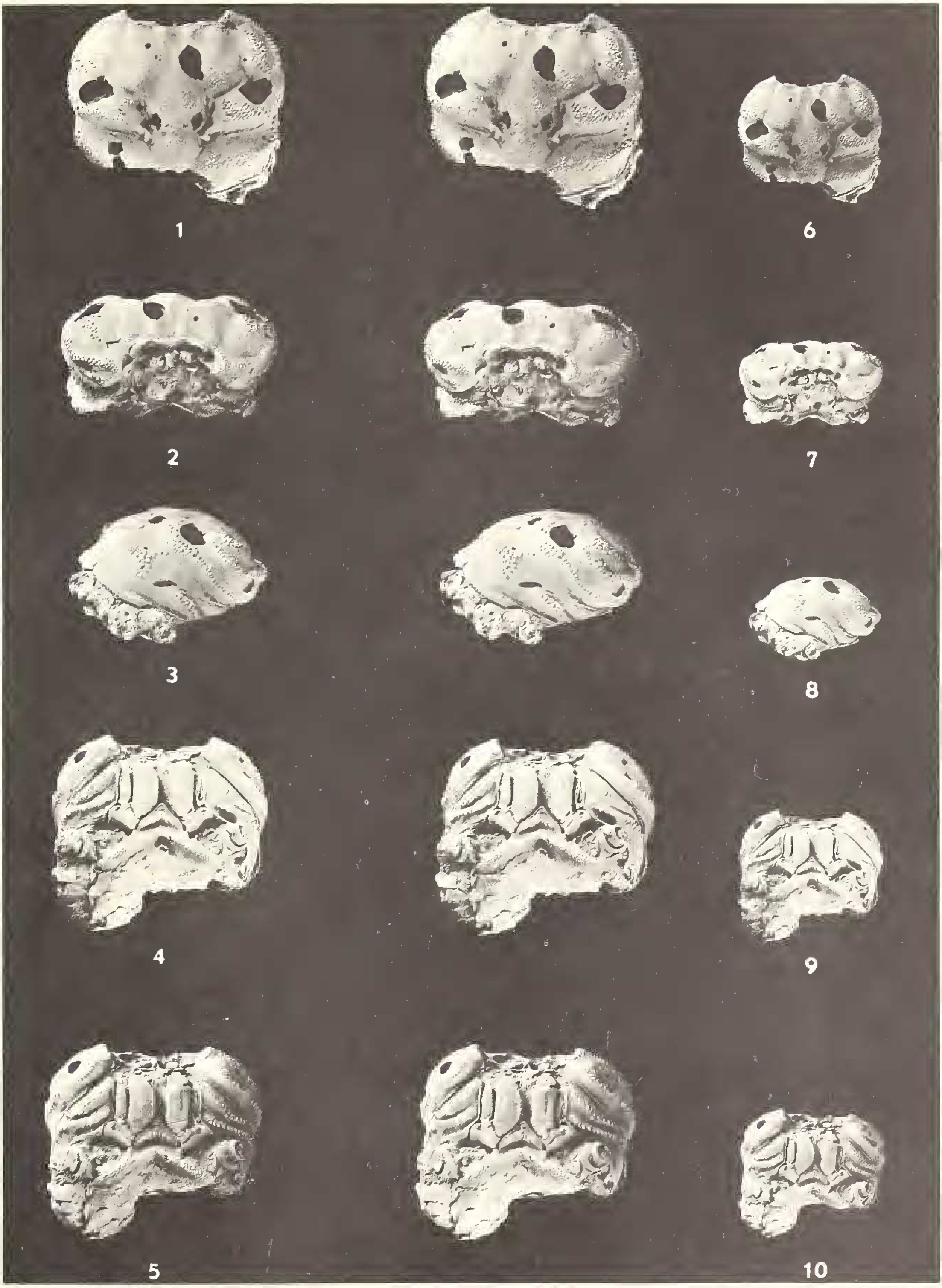


TEXT-FIG. 1. Preservation of decapods. *a*, *b*, dorsal and lateral views showing lineae (pleural sutures) of *Paromola cuvieri* (Risso) (from Glaessner 1969, p. R406); *c*, position of crab (*Carcinides maenas*) buried alive; *d*, *e*, Salter's position of moults of *Potamon quenstedti* as is shown by lower part of carapace remaining attached to the sternum (after Schäfer 1951); *f*, position of lobster moult (*Hoploparia longimana* (Sow.) from Glaessner 1929).

Fossilization. The moult, or shed exoskeleton, is capable of being fossilized, just as is the living brachyuran. Schäfer (1951) has summarized the conditions and processes of the fossilization of brachyurans. The position of the fossil in the sediment and the arrangement of the skeletal elements are very important in the determination of the condition of the animal at the time of its burial.

EXPLANATION OF PLATE 122

Figs. 1–10. *Dakoticancer overanus* Rathbun, specimen 4–369, Mobridge Locality, Mobridge, South Dakota. 1–5, ×1·5, stereo, Figs. 6–10, ×1. 1, 6. Dorsal. 2, 7. Anterior. 3, 8. Right side, notice crack along pleural suture. 4, 9. Ventral, anterior-lateral carapace margin, sternal plastron, maxillipeds, and pleural sutures visible. 5, 10. Oblique of mouth frame and anterior of crab showing triangular notch on mouth frame margin which gives rise to the pleural suture.



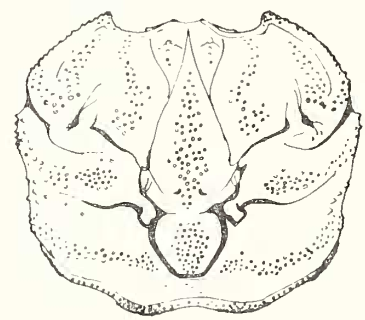
BISHOP, moults of *Dakoticancer*

Brachyurans buried alive attempt to escape from the entombing sediment. The escape attempt consists of a rowing or lifting movement of the appendages. If the escape attempt is unsuccessful, the crab is usually preserved with the appendages frozen in the position of lifting; the legs are commonly raised above the carapace and the chelae are open (text-fig. 1c). Dead crabs and moulted exoskeletons act as passive objects within the limits of their articulation. Physical, chemical, and biological forces act on the crab remains to break them down. After soft tissues decay, corpses and moults react to the forces of destruction in a similar manner. It takes only a few days to decompose the soft tissues. The decomposition of the exoskeleton takes a longer time. The calcareous middle layer breaks down first, within about four weeks (Schäfer 1951). The chitinous inner and outer layers are more resistant to destruction and last for many months.

Corpses and moults can both be found preserved in a characteristic position, Salter's position, in which the carapace is lifted and flipped forward, making an angle of about 90° with the sternum (text-fig. 1 *d*, *e*). Moults are distinguished from corpses by noting that the carapace has split along the pleural sutures, and the parts of the carapace lying outside of the pleural sutures are still attached to the sternal plastron (marked by an 'X' in text-fig. 1 *d*). Fossilized moults of *Ranina*, *Notopocorystes*, *Coeloma*, *Potamon*, and *Macrophthalmus* have been described (Glaessner 1969, p. R431).

DAKOTICANCER

Origin of the specimens. Abundant fossil decapods were collected from the Pierre Shale (Upper Cretaceous, Maestrichtian) from three localities in South Dakota: Creston, Thomson Butte, and Mobridge. The Pierre Shale is a thick body of fine-grained clastic rocks, mostly shales, siltstones, and calcareous shales interbedded with thin bentonite beds. Fossils are numerous and well preserved in calcite and siderite concretions but rare in the shale itself. Ammonites provide the basis for a biostratigraphic zonation (Gill and Cobban 1966). Decapods are preserved in apatite concretions distributed through intervals of shale ten to twenty-five feet thick and continuous over areas of six to six hundred square miles. Fossil assemblages from the three localities are similar, and are dominated by the brachyuran *Dakoticancer overanus* Rathbun 1917, the epifaunal bivalve *Inoceramus*, the nektonic ammonite *Baculites*, and the feces of soft-bodied burrowing organisms. Many other organisms are present but less common. *Dakoticancer overanus* is the most abundant fossil, and this recurring suite of fossils is termed the *Dakoticancer* Assemblage. The consistent faunal composition, similar mode of preservation, the age distribution of the decapods, and the lack of scavenging suggests that the fossils are the remains of mass killings of a recurring decapod community.



TEXT-FIG. 2. Line drawing of the carapace of *Dakoticancer overanus* Rathbun (Drawn by R. Gries).

Morphology of Dakoticancer. The squarish-oval carapace of *Dakoticancer overanus* (text-fig. 2) is dominated by longitudinal ridges ahead of the cervical furrow and on the sagittal ridge and by transverse ridges and grooves on the branchial regions. Two transverse branchial ridges are separated by a broad furrow. A sharp line lies just behind the anterior ridge. The two ridges swing forward as they approach the lateral wall of the carapace. The anterior ridge continues on the lateral wall forward and downward then swings upward to the lower edge of the orbit. The posterior branchial ridge splits at the edge of the lateral wall of the carapace. One short branch runs anteriorly to the sharp line just behind the anterior branchial ridge. The other branch runs backward and downward about one-third of the distance to the posterior-lateral margin. The second ridge begins again on the lateral wall of the carapace, paralleling the carapace edge until it disappears near the lower end of the mouth frame. A third ridge is found between these two ridges on the anterior-lateral wall of the carapace. It extends to near the upper end of the mouth frame. Between the lower edge of the orbits, where the anterior branchial ridge terminates, and the upper part of the buccal frame, where the middle ridge terminates, there is a small triangular notch in the buccal frame margin. The pleural suture begins at the posterior apex of this notch and runs in the depression between the upper and middle ridges, through the furrow between the two branchial ridges until it crosses the trend of the posterior branchial ridge on the smooth area below the point where the ridge splits, and continues on to the posterior-lateral margin.

Moults of *Dakoticancer*. Of the more than 4,000 specimens of *Dakoticancer* collected twenty specimens of moults were found. All were drawn from 2,500 decapods collected near Mobridge, and are from the Zone of *Baculites grandis* Hall and Meek (Maestrichtian).

Each moult is preserved in Salter's position, but with the carapace flipped upward and completely overturned (text-fig. 3). This position has not been described as the Salter's position before and therefore expands the meaning of the term for decapods. In most specimens the carapace is also rotated about a vertical axis and about the sagittal axis.

That these specimens are indeed moults is proved by several specimens on which the part of the carapace outside the pleural sutures still rests on the sternum (Pl. 123, figs. 8–13). The carapaces are apparently rotated because the mode of attachment of the middle part of the carapace to the moulting foundation was non-existent or very weak. As the crab escaped from its old exoskeleton the carapace was probably flipped forward, stopping in a vertical position as is normal in Salter's position. Any water currents made by the escaping animal were enough to disturb the equilibrium and the middle part of

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EXPLANATION OF PLATE 123

Figs. 1–13. Exuviae of *Dakoticancer overanus* Rathbun. All figures ×1, stereo.

Fig. 1. Ventral view of specimen showing left side of sternum and carapace which has flipped over and rotated 80°, specimen 4–1039 (USNM 173394).

Figs. 2–3. Female with carapace flipped over and rotated about 33°. 2. Dorsal view looking down into inside of carapace. 3. Ventral view, specimen 10–120 (USNM 173395).

Figs. 4–5. Female with carapace flipped over and rotated about 10°. 4. Dorsal. 5. Ventral, specimen 4–395 (USNM 173396).

Figs. 6–7. Specimen with carapace flipped over and rotated 95°, specimen 4–2002 (USNM 173397).

Figs. 8–10. Female with carapace flipped over and rotated 10° clockwise. 8. Dorsal. 9. Ventral. 10. Anterior showing portion of carapace outside pleural suture still on sternum, specimen 4–1131 (USNM 173398).

Figs. 11–13. Male with carapace flipped over and rotated 106° counterclockwise. 11. Dorsal. 12. Ventral. 13. Anterior showing portion of carapace outside the pleural suture still on the sternum, specimen 4–824 (USNM 173399).